THE PLANT DISEASE REPORTER

Issued By

CROPS RESEARCH DIVISION

AGRICULTURAL RESEARCH SERVICE

UNITED STATES DEPARTMENT OF AGRICULTURE

VERTICILLIUM HADROMYCOSIS OF DECIDUOUS TREE FRUITS

K. G. Parker

Supplement 255 May 15, 1959

The Plant Disease Reporter is issued as a service to plant pathologists throughout the United States. It contains reports, summaries, observations, and comments submitted voluntarily by qualified observers. These reports often are in the form of suggestions, queries, and opinions, frequently purely tentative, offered for consideration or discussion rather than as matters of established fact. In accepting and publishing this material the Crops Research Division serves merely as an informational clearing house. It does not assume responsibility for the subject matter.

THE PLANT DISEASE REPORTER

MYCOLOGY AND PLANT DISEASE REPORTING SECTION

Crops Protection Research Branch   Plant Industry Station, Beltsville, Maryland

VERTICILLIUM HADROMYCOSIS OF DECIDUOUS TREE FRUITS

K. G. Parker

Plant Disease Reporter
Supplement 255   May 15, 1959

CONTENTS

VERTICILLIUM HADROMYCOSIS OF DECIDUOUS TREE FRUITS

K. G. Parker[1]

Abstract

The literature on Verticillium hadromycosis as it affects stone and pome fruits is reviewed and the information discussed as to its bearing on development of the disease and its control. Literature on the disease on other crops is included when the information may help to understand the development and control of the disease on trees.

This disease is world-wide in occurrence on stone fruits and all species grown commercially for fruit crops are susceptible. Among the pome fruits, quince appears to be susceptible, with pears and apples only doubtfully so.

The best control available is rotation with non-susceptible crops. If susceptible crops have been grown on soil where the planting of stone fruits is planned other crops should be grown for several years before the trees are planted. Susceptible weed hosts should be kept down both before and after the trees are planted.

Needs for research are discussed. Cultural treatment as it influences the survival of infected trees is included in the list of factors considered. The influence of soil conditions and antibiosis on the development and maintenance of inoculum seems to offer considerable promise for study.

An interesting relation that is evident in the literature is the rootstock-scion combination. Instances are described in which the top is more susceptible than the rootstock, as with apricot on plum root, and the reverse condition, in which the tree fails because of of infection in the root although the scion is only mildly or not at all susceptible, as with pear on quince root.

INTRODUCTION

Vascular wilt or hadromycosis (104), caused by species of Verticillium, affects a wide variety of plants belonging to many genera. Among these the stone fruits stand out as highly susceptible. The literature on the disease as it affects this group has not been reviewed since Rudolph's monograph (104) was published. Using that monograph as a starting point, an attempt is made in the present review to bring together all references to Verticillium wilt in the genus Prunus not listed by Rudolph and to discuss the disease as it affects members of that genus. Frequent reference is made to the monograph and to the papers cited by Rudolph when necessary to make the discussion complete. The very limited literature on Verticillium hadromycosis on pome fruits is reviewed also.

Along with this an attempt is made to discuss the possible pertinence of information obtained in studies on other susceptible crops to Verticillium wilt as it affects the tree fruits. This includes primarily epiphytology, and control by sanitation, crop rotation, and soil fumigation. The development of resistant varieties is not discussed because all investigations on resistance have been on cotton, tomato, and other herbaceous or semi-herbaceous plants and are of interest primarily in connection with the particular crops concerned. The toxin hypothesis of causation of wilt has been recently reviewed (21) and is not discussed here.

---

[1]The literature reviewed in this paper was read and the first draft of the paper prepared during the winter of 1957-1958 when the author was temporarily on the staff of the State Experiment Stations Division, Agricultural Research Service, United States Department of Agriculture. Grateful acknowledgment is made of the guidance of Dr. C. L. Lefebvre and the suggestions made by various members of the staff of that Division, and of the fine cooperation of the staff of the United States Department of Agriculture Library.

The manuscript was critically reviewed by Dr. W. D. McClellan and Dr. G. C. Kent, to whom the author is grateful.

Chemotherapy is omitted because it does not appear to offer immediate promise of control.

In the discussion that follows the different headings, therefore, are understood to refer to Verticillium wilt and hadromycosis as it affects tree fruits belonging to the genus Prunus and to the sub-family Pomideae of the family Rosaceae. The hosts listed conform with the names given in Rehder's Manual and Bibliography (96, 97). Names given by the authors of the papers cited, however, are copied unless changes can be made without chance of error.

The name of the species of Verticillium when given is that used by the author of the study referred to. In many cases a species name is not given in the original publication, and no attempt is made to supply one here. This question will be discussed briefly elsewhere in this review.

Literature surveyed: To search for titles the following journals were examined:

Review of Applied Mycology -- Volumes 7 (1928) through 36 (1957).
Biological Abstracts -- Volumes 3 (1929) through 29 (1955).
U. S. Department of Agriculture, Bibliography of Agriculture -- Volumes 19 (1955); 20 (1956); 21 (1957); and 22, no. 1 (January, 1958).
American Journal of Botany -- Volume 40 (1957).
Annals of Applied Biology -- Volume 45 (1957).
Phytopathologische Zeitschrift -- Volume 28, nos. 3 and 4; 29, nos. 1 through 4; and 30, no. 1 (January through October, 1957).
Phytopathology -- Volume 47 (1957).
Plant Disease Reporter -- Volume 41, nos. 1 through 10 (January through October, 1957).
Tijdschrift over Plantenziekten -- Volume 63, nos. 1 through 5 (January through August, 1957).
British Mycological Society Transactions -- Volume 40 (1957).
Zeitschrift für Pflanzenkrankheiten (Pflanzenpathologie) und Pflanzenschutz -- Volume 64 (January through May, 1957)

Inspection of this list will indicate the plan followed. The abstracting journals were examined beginning early enough to furnish references to papers overlapping those cited by Rudolph (104). This was determined by checking for duplications with Rudolph's citations. Biological Abstracts was examined through the last volume that had an index and the Review of Applied Mycology was examined through one additional year (1957). The examination of The Bibliography of Agriculture was started with 1955, to overlap the latest coverage of the abstracting journals. The original journals were examined for the year 1957 in so far as they were available. Complete volumes which coincide with the calendar year are listed as such, and where only part of the volume was seen or where the volume does not coincide with the calendar year the period covered is indicated.

A part or all of the 1957 numbers of a few additional journals were examined but are not listed because no papers on Verticillium wilt were listed in the numbers seen.

NAMES OF THE DISEASE

The name Verticillium hadromycosis, as explained by Rudolph (104), appears to be the best descriptive brief term available, but the term Verticillium wilt has gained such wide usage that it will be used for the most part in this review, particularly when referring to the work of an investigator who uses the term. It will be understood to include all aspects of the disease: tracheomycosis, hadromycosis, "black heart", defoliation, and yellowing, as well as true wilt.

SUSCEPTS

An attempt is made in the discussion of each species or group to cite all available information on history and range and to cite all reports of the disease published after those listed in Rudolph's monograph. Symptomatology on the different species of stone fruits will be discussed in a separate section.

Stone Fruits

All members of the genus Prunus commonly grown for fruit production are susceptible to Verticillium wilt.

Almond (Prunus communis Arcang.). According to Rudolph, the first report of Verticillium wilt on almond was made by Czarnecki from California in 1923, and Dufrenoy and Dufrenoy (38) reported it from France in 1927. The latter authors observed the mycelium in wood vessels and isolated Verticillium dahliae Kleb. but did not describe inoculation experiments. Carter (23) isolated V. albo-atrum Reinke & Berth. from Prunus communis in Illinois, and Brien and Dingley (18) reported V. dahliae on this species in New Zealand.

While there is little question of the pathogenic relation of Verticillium to the disease on almond in the earlier reports it is important that the point be tested. In 1931, Joessel and Bordas (66) reported successful inoculations to 2-year-old almond trees with V. dahliae. Also in France (3), V. dahliae isolated from apricot was successfully inoculated into almond with even more rapid development of decline symptoms than on apricot, the source of the isolate. Hutton and Morschel (57) inoculated tomato plants growing adjacent to almond trees and the disease developed on the trees within 12 months.

Finally, Day (30) reported the disease on apricot nursery trees growing on almond roots, listed in this section because infection probably in most cases is through the roots.

Apricot (Prunus armeniaca L. and P. mume Sieb. & Zucc.). According to Rudolph (104) Verticillium wilt was first reported on apricot in 1916, with definite proof of susceptibility published in 1923. A more recent inoculation test was made by Joessel and Bordas (66) who reported successful inoculations with V. dahliae to 2-year-old apricot trees. Rudolph's reports were from California, and the disease was reported from Canada and from France in 1927. Since that time additional reports have been made from British Columbia, Canada (27, 28), Washington State (14, 46), Italy (15, 29, 47, 77), and from Hungary (11, 56). Additional reports from France will be discussed under the discussion of the relation of Verticillium to apoplexy. The disease has assumed importance in Australasia. Cheney (26) described the disease from Victoria and, although the symptoms differed somewhat from those described in Czarnecki's original description, there appears to be no reason to doubt the authenticity of this report. Later reports were from Victoria (4, 43) and New South Wales (57) on the Australian mainland, from New Zealand (5, 16, 17, 67, 98, 107), and from Tasmania (119).

According to Weiss and O'Brien (120) the disease has been reported on Prunus nume from California, Utah, and Washington.

Day (30) apparently considers the apricot rootstock more susceptible to "blackheart", caused by V. albo-atrum, than other rootstocks of stone fruits used in California.

Many reports have been made from Europe of a serious disease of apricots called "apoplexy". Certain of the more recent reports have indicated Verticillium wilt to be part of this disorder. The chief characteristic of apoplexy is that a part or all of the affected trees dies rapidly.

Joessel (65) found in trees -- in both orchards and nurseries -- in a declining condition, a brown to black discoloration in the wood, and he microscopically identified Verticillium in the tissue. He associated the discolored tissue with mechanical wounds, including in the case of the nursery trees the cut made to remove the portion of the stock above the inserted bud. Curzi (29) referred to Verticillium wilt as described on peach by previous workers as a partial explanation for apoplexy symptoms on apricot in Italy. Sarejanni (105) isolated a microsclerotial form of V. albo-atrum from 5- to 7-year-old apricot trees in Greece with symptoms of apoplexy, and has isolated the same form of this fungus from potato in the same area. Potato and other susceptible crops are often planted between rows of apricot. Chabrolin (24, 25) found more discoloration in the inner bark of affected trees than in the woody tissues and, therefore, considers Verticillium unimportant to this disorder. Joessel and Bordas (66) published additional observations indicating a symptomatology similar to that caused by Verticillium and isolated V. dahliae from affected trees.

More recently, Rieuf (100), Delmas (31), and Morvan (90), have published studies indicating a strong belief that Verticillium wilt is one of several causes of apoplexy. Morvan recognizes three forms of apoplexy. One is characterized by necrosis of bark in the crotches of the trees. His photographs resemble at least in part a type of injury usually attributed in the United States to low winter temperatures, particularly on trees that grow late in the autumn and are not fully "matured". Another form is associated with tracheomycosis and Verticillium is isolated from such trees. Affected trees wilt in July and turn pale or yellow, the leaves drop, and the wood is discolored. It occurs where the trees are planted in old lucerne fields

or where potatoes, tomatoes, or strawberries had previously been grown. The third and most important type of apoplexy is associated with necrosis in the bark instead of in the wood, and therefore probably has no relation to the Verticillium wilt disease.

At any rate, it appears very likely that Verticillium wilt causes a significant part of the disease of apricots generally termed "apoplexy" on the European Continent.

Cherry (Prunus spp.). Rudolph credits van der Lek (113) in 1918 with the first report of Verticillium hadromycosis on cherry, the first definite report of the disease on any kind of stone fruit. He further reviews work by van der Meer (114, 115) in which V. albo-atrum and V. dahliae were isolated from various species and varieties of cherry and from several herbaceous hosts and cross inoculations were made. Isolates from sour and sweet cherry and from Prunus mahaleb L. were successfully inoculated into cherry and into certain herbaceous hosts. Inoculations to cherry with isolates from herbaceous hosts likewise were successful.

At the time Rudolph prepared his monograph the disease was known on cherry in Holland, Czecho-Slovakia, Denmark, France, and Corsica. Since that time it has been reported on sour cherry in Germany (137) and on Morello [sour] cherry in England (138). McKeen (84) observed symptoms on both sweet and sour cherry on the Niagara Peninsula in Ontario, Canada. The disease was reported on both sweet and sour cherry in British Columbia (27, 28) and on sweet cherry in California (132) and in Washington State (14). McIntosh (81) reported a particularly severe occurrence on sweet cherry in British Columbia.

Donandt (36), in a host range study, obtained infection with severe wilt on P. mahaleb following artificial inoculation with isolates from several hosts, including certain weeds and Prunus domestica L.

Dufrenoy and Dufrenoy (38) isolated the fungus from St. Lucie cherry [P. mahaleb], made successful cross inoculations with V. albo-atrum from potato and cherry, and obtained infection with the cherry isolate on tomato.

Peach (Prunus persica Batsch.). Rudolph (104) described experiments in which successful inoculations with Verticillium were made from peach to eggplant by C. M. Haenseler in New Jersey, from peach to tomato by M. F. Barrus in New York, and from peach to Myrobalan seedlings, tomato, and raspberry by Rudolph. Apparently no one has successfully inoculated peach. In later reports McKeen (83) made inoculations with isolates from peach and other plants to a host range (not including peach) and obtained infection with the peach isolates on these hosts about equal to that obtained with other isolates.

In addition to the report from New Jersey in 1922, that from New York, and the widespread occurrence in California (104) the disease has subsequently been reported on peach from the following states: New York (88), Oregon (120), and Washington (14). It is known in Canada in Ontario (83, 134, 135) and British Columbia (27, 28). It has been reported from New Zealand (6, 18, 67, 107). In Europe it has been recorded from France (42, 65). From Holland van Koot (117) reported Verticillium attack on peach grown under glass in a house where tomato had been attacked by Verticillium "sleeping sickness". There is a strong probability that peach is affected by Verticillium in Greece (105). Pollacci (93) reports from Italy "tracheomicosi" on peach apparently caused by a species of Verticillium. Atanasoff et al. (10) list V. albo-atrum from P. persica in Bulgaria.

Plum (Prunus spp.). Rudolph (104) credits Czarnecki with the first report of the disease on plum in 1923, on Myrobalan seedlings, although inoculation experiments were not made until his own work reported later (103). He made successful inoculations to Myrobalan seedlings with isolates from Myrobalan, tomato, apricot, peach, and raspberry. Dufrenoy and Dufrenoy (38) reported successful cross inoculations with isolates from raspberry and plum. They did not specify the kind of plum that was the source of the fungus used but described the disease on P. domestica L. It seems, therefore, that pathogenicity of Verticillium to the European plum is well established.

Wollenweber (137) in Germany reported the isolation of Verticillium from P. domestica which showed blackish-brown discoloration in the wood. Curzi (29) in Italy observed partly defoliated trees in which he identified the Verticillium fungus in the tracheids, apparently by microscopic examination. Atanasoff et al. (10) isolated V. albo-atrum from P. domestica in Bulgaria. Pollacci (93), also in Italy, states "tracheomicosi" is equally severe on plum and apricot. Husz (56) in Hungary isolated V. albo-atrum from Myrobalan nursery trees with symptoms of wilt and black heart. Marchal (85, 86) in France reports apoplexy rather common on plum with V. albo-atrum found associated with it. Van Koot (117) describes the

disease on plums along with peach under glass in Holland. Keyworth (70) described the disease as caused by V. albo-atrum on a single Victoria plum tree in Kent.

Carrera (22) observed wilt on P. domestica in Argentina and isolated Verticillium sp. from affected trees. Day (30) found verticilliosis occasionally on trees on Myrobalan rootstock in both orchard and nursery but stated that it is more severe on apricot rootstock than on Myrobalan, however. Blodgett and Twomey (14) observed wilt on two young trees of Stanley prune (P. domestica).

The disease has been reported from New Zealand on plums (6), but Smith (107) indicates that it is comparatively unimportant.

Goidánich (48) reported the disease on the Burbank variety (P. salicina) near Bologna, Italy, and Gaudineau (42) states that Japanese plums are often attacked in France although it is difficult to determine from her report whether verticilliosis is the primary cause.

While some of the earliest successful inoculation experiments on stone fruits were made on Myrobalan seedlings, apparently plums are generally less susceptible than are apricots. M. Dufrenoy (39) and Rieuf (100) describe apricot on plum rootstock in which the apricot portion of the tree is killed leaving the plum understock comparatively unaffected.

Miscellaneous Species of Prunus. Prunus davidiana Franch resembles peach and is used primarily as an ornamental. Some use is made of it as an understock. Ghillini (44) observed one tree with wilt and with discoloration in the wood, from which he isolated a Verticillium which produced sclerotia in culture. His photographs of a young twig and of a cross section of the lower trunk show clear symptoms usually considered as characteristic of Verticillium hadromycosis.

According to Weiss and O'Brien (120) the disease has been reported on Prunus laurocerasus (Mill.) Ait. and P. lusitanica L., English cherry laurel and Portugal laurel respectively.

Sommer (109) reports the disease on nursery trees of stone fruits but does not name the species.

Pome Fruits

Rudolph (104) did not describe the disease on pome fruits and, therefore, presumably the earliest reports of Verticillium attack on this group are cited in the present review.

Apple (Malus pumila Mill.) In a list of new records from Bulgaria in 1932, Atanasoff et al. (10) listed V. albo-atrum as found on Pyrus malus, but they did not specify the tissue involved nor describe symptoms. That species is listed, however, in their report along with other hosts known to be suscepts of this pathogen. Since Verticillium has been isolated from the bark of trees, probably growing saprophytically, Atanasoff and his associates may have obtained the fungus from apple bark and a pathogenic relation is not necessarily indicated.

In a study of decay of apple fruits Huber (55) isolated 58 species or forms of various genera of fungi from the surface of sound fruits, with which he was able to cause decay by artifical inoculation to sound fruits. Of these forms, nine belonging to six genera had not previously been reported as causing decay of apple fruits. Three of the new forms were listed as belonging to Verticillium with no indication of the species. On the other hand, Adams and Tamburo (1), in an extensive study of apple fruit rotting, failed to find any form of the genus Verticillium in naturally-occurring lesions on the fruit. They limited their study to isolates from already-existing lesions on fruits taken directly from the tree or on freshly-harvested fruits on the packing lines. They found representatives of 22 fungous genera capable of causing rot, as based on artificial inoculations, but Verticillium was not among them.

As it stands, further evidence of pathogenicity is required before apple can be considered as a suscept of Verticillium wilt [2].

Hawthorn (Raphiolepis spp.). Wilhelm et al. (133) in 1955 reported the isolation of V. albo-atrum from the vascular tissue of Raphiolepis indica (L.) Lindl. (India hawthorn) and R. umbellata var. integerrima Rehd. [R. umbellata f. ovata (Briot) Schneider] (Yeddo hawthorn).

[2] Since the preparation of this review a report was made that indicates apple may be slightly susceptible. R. W. F. Sewell and H. H. Glasscock (Plant Pathology 7: 76. 1958) isolated Verticillium from apple wood with discolored sectors on trees that bore dead blossom "trusses". Inoculation into young trees caused vascular discoloration but no wilting.

The plants were growing in two areas of the University of California campus at Berkeley and in a private garden. They showed "...unilateral dying of branches, yellowing, browning, and casting of lower leaves, and pronounced brown to black vascular discoloration."

Pear (Pyrus communis L.). In 1933, Wormald and Harris (139) reported that many young pear trees on the quince clonal rootstocks Malling types A and C "failed altogether" or the foliage on them turned yellow and withered. Discolored tissue was present in the wood of the stocks and V. dahliae was isolated from them. They suggest the stocks probably were diseased when they were planted for propagation of the pears but did not make any comment on discoloration in the wood of the scion nor fungous invasion of it. The same workers (140) in a later report described symptoms "characteristic of Verticillium wilt" in the rootstock just above the roots of 2-year-old pear trees on Malling Quince type C rootstock. They describe clearly delimited blue green discolored areas in the wood with fungous hyphae in the vessels and isolated V. dahliae from this tissue. Less than 1 percent of the trees in the nursery where this occurrence was encountered were said to have "succumbed". There is no mention of inoculation experiments in either of these two reports.

In 1931, Montemartini (89) at two sites in Italy observed pear trees on which during the summer the leaves became reddened. From one of these two sites he obtained material for study and found the wood affected by a tracheomycosis and isolated V. albo-atrum from this material. He stated that the fungus was localized in the wood of the main branches which bore the reddened foliage. Apparently, he did not find evidence of the fungus in the wood of the smaller branches. The rootstock on which these trees were propagated is not indicated and one, therefore, wonders whether it may be quince, the infection having originated in quince roots and moved part way up into the pear top. In any case, this appears to be the first report of Verticillium being obtained from pear wood itself.

In a report from Holland (7), the following statement appears "Anatasting door verwelkeziekte, veroorzaakt door Verticillium dahliae werd constateered bij perezaailingen van het ras Drielse Groen." [Attack by the wilt disease, caused by Verticillium dahliae was diagnosed on pear seedlings of the variety Drielse Groen]. No further explanation is given in this report.

Blodgett and Twomey (14) suggest that Verticillium might be a factor in the very vexing problem of pear decline in Washington State, and Sprague (110) reported the isolation of Verticillium from pear roots. Sprague made isolation attempts by washing root tissue and planting pieces on agar. He considered Pythium debaryanum to be the most likely pathogen obtained. He obtained Verticillium sp. from approximately 10 percent of the samples, but this percentage was approximately the same whether the samples were from trees showing severe decline, moderate decline, or appeared to be healthy. Apparently Sprague did not make inoculations with these isolates and it may be that the isolates of Verticillium obtained were saprophytic forms. The method of isolation used would be likely to select fungi in the outer dead tissue, and according to Isaac (60), weakly pathogenic forms of Verticillium are better saprophytes than are the more strongly pathogenic forms.

Photinia villosa DC. There is a single report from Holland of the isolation of V. dahliae from this species, with no description of symptoms and no statement concerning inoculation tests (7).

Quince (Cydonia oblonga Mill.). In England, Wormald and Harris (139) isolated V. dahliae from discolored wood tissue in "quince layers" with wilting shoots, and, as already discussed, found that young pear trees failed on quince clonal stocks having discolored xylem. In a later report (141) the same workers described "defective" leaf development on Malling Quince C stock plants that had not been budded and observed greenish-black sectors in the wood in cross section. They isolated V. dahliae from this material. They were unable to isolate the fungus from the base of budshoots on budded stock plants similarly affected, but it is not stated whether the budshoots were of quince or pear.

In Belgium, Vanderwalle (116) found a yellowing and defoliation and general sickly condition of quince budlings in their first growing season. The wood was discolored, and a Verticillium was isolated with characters ascribed to V. dahliae. Affected budlings were scattered through the nursery plantings, indicating the possibility of the fungus having been introduced in the budwood. He considered there was evidence that affected material was brought in from France and from Holland, where the disease is known as "het zwart in de kwee" [the black in the quince] . Gaudineau (42) in a general paper on certain diseases of

fruit trees in France describes the disease caused by V. dahliae on cherry, peach, and quince. She states that individual branches wilt suddenly and yellowing and defoliation follow. In cross section, the branches of the trees show reddish-brown color in the vessels, but it cannot be certain that this description in its entirety applies to quince specifically. The paper contains no detailed description of experimental work, but there appears to be no question in the author's mind that V. dahliae causes disease on quince of the hadromycotic type.

Brien and Dingley (19) reported V. dahliae on C. oblonga in New Zealand.

SYMPTOMS

The description of symptoms to follow refers primarily to stone fruits. For the very meager information available on symptoms on pome fruits the reader is referred to the preceding sections on the various species.

Morphologic Symptoms

Symptoms on apricot and on peach are much alike and the following general description represents the development of the disease on these two species. Variations from this more usual symptom picture as they occur on other stone fruits will be described later.

Most writers agree that at first symptoms usually appear on only a part of the tree and may be limited to a single branch at that time. J. Dufrenoy (37) states that a tree may bear chlorotic leaves one year and during early summer the following year have large branches dry up one after the other. A sudden wilting early in the summer is common, although this may not occur until late summer (14). The onset of symptoms probably depends primarily on when water stress becomes acute. The leaves at bases of branches wilt, turn yellow and drop, leaving green leaves on the distal portion of the twigs. Most writers describe this as occurring progressively upward through the tree (67), but Hutton and Morschel (57) state that symptoms appear first on the "extremities" of lateral shoots and leaders. Cheney (26) states that in the year following extensive wilt and defoliation buds on affected branches fail to open and the branch dies, or the flower buds open and set fruit but the fruit drops.

Young trees, 1 to 8 years old, are most seriously affected, and rarely is a tree more than 1 year in the orchard killed entirely (67). This statement seems to hold in general, although over a period of years the tree may lose so much bearing surface from progressive death of affected branches that it becomes unprofitable.

On plum, Keyworth (70) observed that if the leaves were older when attacked they withered and turned brown, but the younger leaves wilted and remained green. Hochapfel (52) described the disease on plum, on which there was no wilt but all buds on older parts of the tree failed to open, the only leaves being on the 1-year-old shoots.

On sweet cherry McIntosh (81) describes a wilt on one or more spurs of the leaders, on 1-year-old wood, with the leaves faded green, and infrequent yellowing. This starts in the lower part of the tree and progresses upward and laterally. Blodgett and Twomey (14) describe similar symptoms, and state that they may appear in July or August. The tree becomes unthrifty, off color, has small leaves, poor fruit size, and recovery is less common on cherry than on apricot. Blodgett and Twomey describe considerable dieback and suckering on cherry, but they do not consider wilt and death of spurs in the main framework of the tree symptoms of the disease.

Most writers describe no necrosis in the bark of affected trees, but Curzi (29) indicates that on affected plum (P. domestica) the bark separates from the wood, and Dufrenoy and Dufrenoy (38) note that the bark becomes necrotic on apricot trees on plum rootstock. In these cases mycelium was observed in the xylem vessels, and it seems likely that direct attack by the fungus occurred only in the wood.

Histologic Symptoms

Most writers agree that there is a brownish-black (greenish on quince) discoloration in the sapwood, in cross section appearing as arcs and dots. Usually more discoloration is observed in the wood of the trunk and main framework than in smaller twigs (57, 107). The discoloration is said to be darker in the older wood than in the young twigs (98).

For a full description of histologic symptoms on stone fruits and their development the reader is referred to Rudolph's monograph (104). Little has been added to our knowledge of the subject since that monograph was published.

ECONOMIC LOSSES

Judging from the number of reports in the literature, apricot apparently is damaged more by Verticillium hadromycosis than is any other tree fruit species. Whether this is because of greater susceptibility or chance of inoculation cannot be determined with the information available. Hutton and Morschel (57) report that the disease was identified in New South Wales first on apricot in an orchard planting of 250 trees and when first determined in 1948, 32 trees had been killed and many more were seriously injured. Renouf (98) in the initial report from New Zealand stated that one-third or more of the trees had been removed in some orchards because of Verticillium wilt. Smith (107) indicates that it is increasing in New Zealand since its discovery there in 1945 but that the overall losses are still less than 1 percent. Wade (119) considers the disease serious on apricot in Tasmania.

It appears that generally Prunus armeniaca is more susceptible than the commonly used plum rootstocks because of the reports that the apricot top growing on a plum rootstock is killed and the understock continues to grow and produce new shoots. Numerous descriptions of this condition appear in European literature, among them Dufrenoy and Dufrenoy (38).

Mills (88) described an occurrence of Verticillium wilt in 2-year-old peach trees in which 32 of 45 trees were affected. June (67) finds the disease widespread on peach in the Hawke's Bay district of New Zealand. Various other reports of the disease on peach either do not emphasize its severity or indicate that it is of minor importance. Day (30) received conflicting reports from different nurseries concerning various kinds of trees growing on peach and other rootstocks. Some reported more Verticillium wilt on apricot and peach rootstock than on Myrobalan, while others reported more disease on trees growing on apricot and Myrobalan roots than on peach and almond.

McIntosh (81) described an occurrence of Verticillium wilt on 3-year-old sweet cherry seedlings in British Columbia in which 202 of the total of 220 trees in the planting were affected. An interesting feature of this outbreak was that no known susceptible crop had been grown on this land, as it had been maintained as a stone fruit planting with weed ground cover. Wilhelm et al. (132), on the other hand, reported the disease on sweet cherry trees propagated on both Mazzard and Mahaleb rootstock with symptoms similar to those described by McIntosh, but with no instance of concentrated occurrence such as he reported. This was true in spite of the fact that some of the plantings examined had been made where tomato had grown.

Plum rootstock (Myrobalan) apparently is rather susceptible. Rudolph (104) states that this rootstock often is made unfit for propagation purposes by Verticillium infection. Yet, although many reports of the disease on plum are found in the literature no clear statement indicating a serious occurrence on any of these species has appeared. Pollacci (93) stated that "tracheomicosi" was severe on plum as well as apricot. We cannot be entirely sure he meant Verticillium although this seems likely, and no figures are given. Then there is the statement by Day (30) previously referred to that some nurserymen reported more Verticillium wilt on apricot on Myrobalan rootstock than on peach or almond.

A few additional reports are available on the occurrence of the disease in nurseries, such as those of Wollenweber (137) and Day (30), neither of which provides any clear statement as to just how severe the disease may be.

Recovery from Verticillium wilt symptom expression appears to be rather common, but cannot be depended upon. Wade (119) suggests severe pruning of affected apricot trees to promote recovery, although the effect may be only temporary. Hutton and Morschel (57) indicate that less severely affected trees of apricot may make partial recovery after removal of affected branches but that their life cannot be predicted. Blodgett and Twomey (14) report that apricot may be killed but usually only part of the branches will be lost and that suckering from lower parts will rebuild the tree. It may be that suitable fertilization might help such trees, as has been reported for maple (111), but in most orchards this does not appear to be promising as a control measure.

Of particular concern is the fact that most reports indicate that it is the young trees -- less than 10 years old -- that are most likely to be affected.

Secondary Pathogens Add to the Injury

A discussion of economic losses would not be complete without a statement concerning other pathogens that may be enabled to attack a tree because of previous attack by the Verticillium wilt pathogen. M. Dufrenoy (39) in a general discussion of apoplexy of apricot indicated that so long as the cambium remains alive in trees containing infection by Verticillium they

can continue to grow. Rapid death of the tree or branches follows loss of the cambium, which may be caused by Verticillium itself or by secondary fungi or by insects that are able to attack because of the weakening by Verticillium. In another report from France (2), some of these secondary fungi are named as Fusarium, Coryneum, and Alternaria.

Willison (134, 135) found that Verticillium infection of peach was one of several factors that provided infection courts for the establishment of cankers caused by two species of Valsa. His data indicate, however, that "verticilliosis" was the least important of the several conditioning factors listed, it being responsible for 3 percent of the cankers examined in 1931 and 5 percent in 1932.

Verticillium Hadromycosis and Winter Injury

Zeller (142), working with cane fruits, found that plants infected by this disease suffered greater injury because of low temperatures in winter than did uninfected plants. It seems likely, therefore, that diseased trees would suffer from winter injury, and probably that is the chief reason for the failure of buds to open as reported by several workers.

ETIOLOGY

Name and Classification of the Pathogen

It is not within the province of this review to attempt to settle the question of classification of the species of Verticillium involved in hadromycosis. Rudolph (104) gives a thorough discussion of the question up to the time of his review.

Most reports of Verticillium hadromycosis of tree fruits list V. albo-atrum or V. dahliae as the cause, with the latter probably being mentioned the more frequently. This question is pertinent because of the importance of microsclerotia to persistence of the fungus in the soil. That is, the chief difference given between the two species is that V. dahliae produces microsclerotia and V. albo-atrum does not (71). Recent workers who have given attention to this question and who favor retaining the species V. dahliae as distinct from V. albo-atrum include Berkeley et al. (12), Isaac (59), and Robinson et al. (102). Papers in which the view supporting combination V. dahliae with V. albo-atrum is expressed include Wollenweber (137), McKeen (83), Wilhelm (122), Presley (94), and Caroselli (21).

The influence of temperature on growth and distribution of the pathogen is significant. Robinson et al. (102) found that the resting-mycelium type had a lower temperature maximum for growth than did the pseudosclerotial type, and that the former was the only form found on potato in Wisconsin and eastern Canada while the latter only was found in Idaho. Previous reports have stated that the forms that produce microsclerotia have the higher temperature relations of the two types (59, 79). Edgington (40) found the same relation.

Reports of differences in pathogenicity among different isolates of Verticillium are frequent in the literature, and these differences often are correlated with differences in the resting bodies, microsclerotia, resting mycelium, and chlamydospores (63, 79, 94). The most recent of these papers, by Isaac (63), presented evidence that V. albo-atrum was the most pathogenic of five species tested, V. dahliae was next, and the other species required special nitrogen nutrition to produce a pathogenic reaction.

This whole question of designating the forms of Verticillium that cause hadromycosis and wilt in tree fruits is of considerable importance because of the differences among them in pathogenic relations, persistence in the soil, and other characters. The factors just mentioned will serve as examples of the need for an adequate and usable means of identification of these different forms. It may make little difference whether they are given specific rank or are described as forms within a single species, as suggested by Presley (94). One of the greatest needs in the study of Verticillium hadromycosis is for a careful, thorough investigation of this question, using controlled cultural conditions. If factors such as temperature, pH, nutrients, and light influence the production of morphological structures of any single form, it seems that with uniform controlled conditions it should be possible to establish procedures for distinguishing the different forms (102). If such a study were made, a means of determining forms whenever the need arises would be available.

Life History of the Pathogen

Source of Inoculum. Statements in the literature that the disease in tree fruits is associ-

ated with previous or concurrent growing of susceptible herbaceous crops are so numerous that contrary experience is out of the ordinary and worth mentioning. Outstanding among such reports is the one by McIntosh (81), who reported a very severe outbreak on sweet cherry in a field in which no susceptible crop had been grown. The field had been maintained in weed cover, which may account for the high percentage of infection in the trees.

Hutton and Morschel (57) inoculated tomato plants growing adjacent to young stone fruit trees and infection developed on apricot and almond trees within 12 months. The literature contains many references to studies indicating that debris from diseased plants incorporated in the soil will build up inoculum. Blank and Leyendecker (13), for example, applied diseased cotton stalks to the ground at different times of the year and immediately plowed the ground and at the same time plowed adjacent untreated soil. Disease-free cotton seed was planted in April. Up to 95 to 99 percent infection occurred in the ground where the diseased cotton stalks had been plowed under and none occurred in the check plots. Wilhelm (126) failed to find V. albo-atrum in the rhizosphere of diseased tomato plants or on the plant roots, but in an earlier study (123) he found that on the death of infected plants the fungus invades the pith and cortical tissue and produces microsclerotia there. He reported survival of the fungus for as long as 14 years in one case in soil that had been continuously planted to grains and pasture, and he suggested that the carry-over probably was in the form of microsclerotia. Keyworth (69), working with hop, incorporated diseased bines and soil from diseased plants in clean soil, then made new plantings. Infection where the diseased bines were used as inoculum was 10 times that where soil from diseased plants was used. Wilhelm (123) and others have suggested that microsclerotia or plant debris -- probably containing microsclerotia -- may be blown about by the wind and infest new areas, or at least new areas within a given field.

Inoculation. Surprisingly little study has been made of the natural mode of inoculation and infection with these fungi, particularly on trees. Berend (11) described a small scale experiment in which young apricot seedlings were potted in artificially infested soil and later wounded (method not described), with other seedlings planted similarly but not wounded. Infection developed only in the wounded trees. It is significant that most reports of Verticillium hadromycosis state that infections usually occur in young trees, up to 10 years old but mostly within the first 2 or 3 years from planting. It seems probable that many of the infections are the result of invasion through wounds present on the trees at planting time. It is common practice to make fresh cuts on many roots at the time the trees are planted, to remove dead and broken roots and to shape the root system. This may not be good practice. In fact, it has been found experimentally with another pathogen, the crown gall organism (54), that less infection results if any root-pruning needed is done before time to plant and time is allowed for healing before the trees are planted.

On the other hand, Isaac (58), working with Verticillium infection in sainfoin [Onobrychis viciaefolia], obtained evidence that artificial wounds may not be necessary. He inoculated unwounded roots of small seedlings growing in nutrient culture and studied the development of infection microscopically. He illustrates apparently direct mechanical penetration into root hairs, through the root-cap region into the vascular tissue, and through wounds made by the emergence of lateral roots. He did not follow development of the infection further and there may be some doubt whether extensive invasion of the plant occurs by this means. Furthermore, there is no assurance that infection would occur in this manner under field conditions.

Hutton and Morschel's experiment already described (57) indicates that symptoms may develop on apricot within 1 year or less of the time of inoculation with V. dahliae. Since trees are known to recover from symptom expression it would not be surprising, on the other hand, for a delay to occur in the initial expression of symptoms.

Propagation with Diseased Material. Vanderwalle (116) suggested that the Verticillium hadromycosis pathogen may be carried over into new quince trees in the scionwood. Apparently he did not test the point experimentally, and while other reports of the disease in nursery trees exist no others encountered in this study suggest this means of increase.

Working with roses, Dimock (33) obtained ample evidence that infection on rose plants may be readily obtained by budding with budwood from affected plants. One bud developed into a shoot after serving as inoculum for the plant. Raabe and Wilhelm (95), also working with rose, obtained comparatively high percentage infection by budding with a contaminated knife. A lower percentage infection was obtained by brushing the wound made in removing the stock above the inserted bud 1 month after budding. Likewise, a low percentage of infected plants resulted from the use of buds from infected plants for propagation. More study is needed on

this point, but according to present evidence some possibility exists that fruit trees might be infected if buds for propagation are taken from affected trees.' The relative importance of this source of infection remains to be determined. The question is sufficiently important that a study should be made, taking into account the fact that preventing this means of transmission in nursery practice might add to the expense, and nurserymen cannot afford to follow expensive unnecessary practices.

Inoculation in Pruning. Dochinger (34, 35) was able to transfer the fungus from diseased to healthy maple trees by pruning, with 10 percent infection. Joessel (65) found discolored wood tissue associated with the cut made in removing the top of the stock in nursery trees and isolated *Verticillium* from this tissue. It will be recalled, however, that Raabe and Wilhelm (95) obtained comparatively high percentage infection by budding with a contaminated knife and a low percentage infection by inoculating the lopping cut. The difference may be because the wound made in budding is covered and wrapped to prevent drying out whereas the lopping cut is left open, as in ordinary pruning.

Saprogenesis. McKay (82) found that the fungus lived for 1 year in potato tops buried in soil, but did not obtain evidence of longer persistence. It took more than a 2-year rotation, however, to obtain effective control. Zeller (142), working with raspberry, obtained evidence that infection would progress down the row by root contact after there was time for infected roots to die. Citing McKay's (82) demonstration that roguing of potatoes increased infection on the remaining healthy plants, Zeller postulated that this was because live infected roots were broken in the roguing process. Because the broken roots died more quickly the fungus was able to grow out of them sooner than from intact diseased roots. Keyworth (68) found that the pathogen produced spores in abundance on leaves, stems, and branches of "moribund" plants.

Roberts (101) made an experimental investigation of the hypothesis that the fungus remains within the host plant until after death of the plant. He planted a diseased tomato plant in the center of a crock with four healthy plants around it. After the plants were established he ringed the stems of the diseased ones in part of the crocks. Symptoms appeared sooner in the originally healthy plants in these pots, and a higher percentage eventually became infected than in the pots with the non-ringed diseased plants. He stated that all ringed diseased plants died, but did not comment on the non-ringed ones; presumably they survived.

Luck (78) found that in muck soil the fungus persists at least 4 years (the length of the study) in the absence of known hosts. He reported greenhouse studies showing that survival is not due to saprophytic growth of the fungus but to persistence of microsclerotia. The mycelium and spores did not persist for longer than 5 months. Wilhelm (128) found a light "infection index" in soil from a field planted to tomato once, then to grains and pasture for 8 consecutive years. After 6 additional years, he still was able to demonstrate the presence of the fungus in the soil.

Isaac (60) made an interesting study on the question of survival of different forms in the soil. He added pure cultures grown on wheat grain to the soil and made isolations at intervals. The more pathogenic forms were not recoverable after 6 months, while less pathogenic forms were recovered after about twice as long a period. His suggestion that the more pathogenic forms could not compete with the other soil microorganisms, whereas the less pathogenic forms were better able to compete and to grow saprophytically, seems reasonable. It was interesting that in comparable isolations after long periods in the soil the pathogenic forms took longer to produce measurable growth in the cultures than did the less pathogenic forms. This longer growth period corresponded with the time it took for growth from microsclerotia, and Isaac suggested that the pathogenic forms were present in a resting stage only, whereas the less pathogenic forms occurred in the resting stage and also in the mycelial and conidial stages, having continued to grow saprophytically.

EPIPHYTOLOGY

Soil Factors. Isaac (62) made a thorough literature review on soil factors, particularly moisture, pH, and plant nutrient supply. He concluded that the moisture relations are "very obscure", but his own studies in pot culture with *Antirrhinum* indicated strongly that in dry soil infection is less than in moist or wet soil. Isaac inoculated his plants by adding inoculum to the soil. Caroselli (21), using a more artificial method of inoculation, one that should be more likely to furnish 100 percent infection, obtained more wilt with a lower water content in

the soil than with more moisture. In Caroselli's experiments the influence of soil moisture probably was on development of wilt in the diseased tree whereas in Isaac's work there may have been more influence on the initiation of infection. Nelson (91), working with mint planted in pots in infested soil, obtained a particularly interesting result. With the soil moisture content maintained at a pre-determined level by weight, he obtained more severe disease development at 70 and at 100 percent water-holding capacity than at the intermediate level of 80-85 percent.

Isaac (62) found less disease development with additions of potassium and with the use of ammonium sulfate as the nitrogen source. Caroselli (21), working with maple trees, obtained less disease with use of all forms of nitrogen except sodium nitrate, ammonium sulfate being the most effective. It seems possible that this effect might have been due to a pH relation, since a substantial body of experience indicates less disease on acid soils, although Wilhelm (124) concluded that the disease was not greatly affected by pH within the usual range in California soils. Haenseler (50) working with eggplant, obtained less disease development with the application of sulfur to the soil, without evident injury to the plant, but stated that he did not consider this a practical method of control because the required pH level is too low.

Temperature appears to be rather important, with little or no development at a soil temperature of 85° F or above (106). Wilhelm (123) stated, however, that in unpublished work James Howard, working at the University of California, determined that microsclerotia could withstand a temperature of 120° F for several months. Edgington (40) found a slightly lower temperature range for the non-microsclerotial type than for the microsclerotial type. He indicated that soil temperature was more important than air temperature. For that reason, it seems unlikely that temperature will reach a high enough point to prevent, or perhaps even retard, development of the disease in fruit trees in the Northeast. At the level of most tree roots the temperature has been found rarely, if ever, to reach 85° F even in the hottest days in unusually warm seasons. On the other hand, the higher temperatures and brighter light during the summer create a greater demand for water and, therefore, wilt is more likely to develop in middle or late summer than in early summer.

Antibiosis. Along with several other fungi, Ark and Hunt (8) found that *V. albo-atrum* may be antagonized by *Bacillus vulgatus* and an unidentified bacterium in pure culture. Arnstein et al. (9) found that musarin, an antibiotic produced by actinomycetes, inhibits *V. albo-atrum* and *V. dahliae* at very high dilution. Leben et al. (75) prevented growth of *V. albo-atrum* in culture with helixin extracted from an actinomycete in the soil. Holmes (53) inhibited growth of *Verticillium* sp. in culture with eight of 16 antibiotics tested.

Nelson (91) found that when the fungus was permitted to colonize sterilized soil it caused more wilt in mint planted in the soil than when it was added to natural soil, and he suggested an antibiotic relation. Wilhelm (127) found that several fungi, including *Gliocladium roseum*, added to sterilized soil checked the growth of *Verticillium* or destroyed it. Wilson (136) found *V. albo-atrum* to be a very poor competitor in muck soil, and obtained control of the disease on tomato with antagonistic fungi. Isaac (61) obtained *Blastomyces luteus* as a contaminant in isolating *Verticillium*, and was able to reduce infection by adding *Blastomyces* to the soil which was later infested with *Verticillium* as a means of inoculating plants. Caroselli (21) extracted metabolites that were antagonistic to *V. albo-atrum* in culture from a soil actinomycete and from *Bacillus subtilis*, a common inhabitant of soil.

Wilhelm (125) obtained a lessened disease development by addition of various amendments to the soil, including ammonium sulfate and organic nitrogen sources, and also barley straw. He suggested that, since microsclerotial production is greater in winter when conditions are unfavorable for activity of soil microflora, the pathogen is most vulnerable to competing organisms when the soil temperature is high. The same author (127) was able to inhibit establishment of *Verticillium* by colonizing other fungi on the tomato straw used as a substrate.

Verticillium Hadromycosis and Nematodes. McClellan et al. (80), working in a field heavily infested with the root-knot nematode (*Meloidogyne*), fumigated the soil with a moderate dosage of ethylene dibromide and obtained improved growth of cotton, apparently as a result of nematode control, but observed no influence on Verticillium infection. The incidence of wilt was about equal in treated and untreated plots, approximately 80 percent. De Segura and Aguilar (32) found that in an area with a light infestation of root-knot nematodes substantial reduction in growth of cotton occurred if *V. albo-atrum* was present along with the nematodes. They do not comment on the influence of the nematodes on fungous infection, however, and the difference in growth found may be due primarily to an additive effect of the two organisms.

McKeen and Bosher (84) controlled Verticillium wilt on strawberry by fumigation with methyl bromide but failed with ethylene dibromide. They were working in an area where root lesion nematodes were present, but did not comment on nematode control. When they autoclaved the soil and added Verticillium inoculum to the soil, infection was readily obtained without wounding the plant roots.

There seems to be no evidence, therefore, that lesions made by nematodes provide infection courts for the Verticillium wilt fungus, although damage to the plants by the two types of organism may be additive. The results of McClellan and his associates constitute evidence that there is no synergism such as, they point out, has been shown for nematodes and Fusarium wilt of cotton.

Special Case of Alfalfa. Alfalfa has been included in lists of crops that may be used in rotations to reduce soil infestation with *Verticillium*. Morvan (90) associated *Verticillium* sp. with apoplexy of apricot in trees planted in old lucerne fields as well as where potatoes, tomatoes, and strawberries had been grown. Wollenweber (137) named a new form, *V. albo-atrum* var. *chlamydosporae* f. *angustum*, obtained from alfalfa. Various reports indicate that Verticillium wilt is of some importance in lucerne, it having been described further in Germany (99, 121), in Holland (7, 112), and in England (92). Isaac (64) considers that both *V. albo-atrum* and *V. dahliae* may attack lucerne, and Richter and Klinkowski (99) inoculated lucerne successfully, but none of these reports contain any reference to cross-inoculations of lucerne with isolates from other plants. There still is some question, therefore, whether the fungus attacking lucerne is the same one that attacks other hosts.

Soloveva and Polyarkova (108) observed that cotton following lucerne was affected less by Verticillium wilt than when growing under other conditions, but found cereals to have a similar effect. These workers suggest it is merely a matter of the lucerne not being susceptible. They did not find the disease on lucerne planted in infested soil.

Kononenko (72) presented strong evidence that *V. dahliae* could be lysed by bacteria obtained from many soils or by bits of the soil itself. Brodsky (20) found a high population of infusoria in lucerne soils and was able to prevent growth of *V. dahliae* by adding the infusoria to the cultures. Lysis of the fungus resulted in cultures where the fungus was allowed to grow before adding the infusoria. Control experiments with infusoria added to culture solutions and to soil gave favorable results. There seems to be some question whether this effect is caused by the infusoria or by bacteria that accompany them, but tests with the bacteria alone were not so favorable as when the infusoria were included with the bacteria, or when infusoria were added and an attempt was made to exclude the bacteria. Verner et al. (118) present evidence that *V. dahliae* and other fungi are reduced in soil by infusoria and bacteria.

Leont'ev (76) watered chrysanthemum plants with nutrient solution containing the infusorian *Colpoda saprophila*, the common one in lucerne soils, and obtained complete protection against infection with *V. dahliae*. The addition of bacteria to this material had no added effect, but control with the infusoria alone was complete.

Kublanovskaia (74) found that under cotton culture *Verticillium* accumulated in the soil and the development of mycolytic bacteria was suppressed, and that alfalfa had just the opposite relation.

CONTROL

Cultural Methods and Care of Trees

Rotation and Sanitation. The prevention of infection by sanitation measures is the most effective means at our disposal for control of this disease in fruit trees. Since the fungus is very generally distributed (87) in the soil, and since apparently a substantial build-up in inoculum is necessary before a significant number of infections are to be expected, avoiding the growing of susceptible crops before or after planting the trees appears to be very effective under most conditions. Many, and probably most, writers on the subject suggest that this be done, and the most common crop listed to be avoided is tomato. In fact, Hesse (51), who lists other suscepts as well, in writing about apricots makes the statement that certain other crops named are less dangerous than is tomato because they "seem to develop strains of *Verticillium* which are not likely to cause black heart." In the present state of knowledge, however, it is not safe to plant stone fruits after or concurrently with any crop that is susceptible to *Verticillium*. Those most likely to be encountered in northeastern United States include tomato, potato, pepper, eggplant, strawberry, and raspberry. The host range is so wide that it

would not be feasible to make a complete list.

Unfortunately, severe outbreaks have occurred in the absence of other susceptible crops (81), and the writer has encountered the disease on a number of occasions in trees interplanted in old orchards. Weeds appear to be the most likely cause of the build-up of inoculum in these cases. Smith (107) lists Chenopodium album as common in affected orchards, particularly orchards where tomato had not been grown. He implied that this weed most likely had served to build up the inoculum.

For orchard conditions, Smith (107) recommends that clean cultivation be practiced to keep down weeds and that cereals, grains, and clover be used as cover crops. Also, of course, he cautions that susceptible crops should not be grown as intercrops in the orchard. He further suggests that an area known to be infested be sowed to grass 2 to 4 years before planting again to a susceptible tree species, such as apricot or peach. He suggests that when an annual crop develops the disease, the plant debris be removed as thoroughly as possible. His 2- to 4-year figure between growing of the susceptible crop and planting of a susceptible tree species agrees with many recommendations on other crops for a rotation, while the suggestion that infected plant debris be removed seems particularly pertinent for trial when an orchard planting is contemplated following a susceptible crop and the grower cannot afford to wait several years. Zeller (142) found that two intervening crops (oats and vetch) between plantings of susceptible raspberry or potato gave satisfactory control but that a 4-year rotation was better. Wilhelm (129), however, studied this question by means of his "infection index" technique. He obtained a fairly high index in fields with up to 5 years intervening between the last tomato crop and the index test. With 8 years or more intervening the index was consistently low, with a correspondingly low strawberry plant loss.

Engelhard (41) provides a very thorough list of susceptible crop plants and weeds. Of the weeds listed the following may be named as frequently encountered in New York State orchards: Amaranthus spp., Chenopodium album L., and several species of Solanum.

With the tendency toward the use of some type of non-cultivation in orchards it seems reasonable that a grass or perhaps grass plus clover or alfalfa sod might be used after the trees are well established. During the first few years when the orchard is cultivated it should be kept clean of all weeds until mid-summer, when a non-susceptible cover crop may be planted.

Antibiosis in the Soil. Alfalfa has been found to be susceptible to Verticillium, but since practical experience with this crop in the rotation still seems to be favorable and reports from Russia indicate a clear antibiotic relation with alfalfa, this crop should be reexamined. Perhaps under many conditions the build-up of antagonistic microorganisms on its roots will prevent development of Verticillium spp. in spite of its susceptibility to the fungus.

A promising field for study is the encouragement of the development of antagonistic organisms in the soil. For example, Wilhelm (127) found that Verticillium failed to grow when introduced into natural field soil, grew vigorously in autoclaved soil, grew moderately well in soil treated with chloropicrin, and grew very poorly in soil treated with ethylene dibromide. This could all be explained by the presence of antagonistic fungi. The natural flora in the untreated soil would prevent all growth, the autoclaved soil would contain no other fungi, at least at first, and the soil treated with chloropicrin would have a reduced fungous population as contrasted with that treated with ethylene dibromide, a comparatively poor fungicide.

Soil Fumigation. Wilhelm (130) reported very good results with chloropicrin as a soil treatment for control of Verticillium wilt on strawberry. This material was first reported as effective by Godfrey (45). In an earlier report, Wilhelm and Ferguson (131) found chloropicrin somewhat more effective than chlorobromopropene, a material with which favorable results have been obtained (49, 73). McKeen and Bosher (84) obtained good results on strawberry with methyl bromide but poor control with ethylene dibromide. They state that lesion nematodes were present in the soil and, therefore, it cannot be certain whether ethylene dibromide failed because of lack of fungicidal action or because of poor nematocidal activity.

Any of these treatments should be tested in combination with various soil amendments to improve physical structure, antibiotic activity, and tree vigor. A chemical is needed that is more selective, one that will reduce infestation by Verticillium wilt fungi without destroying antagonists. For example, Nelson (91), working with mint, found that soil treatment with chloropicrin and other chemicals failed to control wilt, and in most cases actually increased it. He also found that more wilt occurred in steamed soil than in natural soil when both were artificially infested with Verticillium. He attributes this result to antagonists in the non-steamed

soil. It may well be that the chemical treatment reduced the population of antagonistic organisms more than that of the Verticillium.

Root Treatment. No reports of direct experimental work with trees have been encountered, but because of the strong probability that many infections occur through cuts made on the roots at planting it seems worth while to reexamine suggestions made in earlier literature that the roots should be treated by dipping in a disinfestant solution (109). This measure should be preceded by soil treatment with formaldehyde. Perhaps with newer materials such a procedure would be more effective.

Fertilization and pH. Apparently, proper fertilization might be expected to improve the chances of recovery of affected trees. Caroselli (21) cites work of others, and describes experiments of his own in which nitrogen fertilization appeared to reduce wilt development in maple. Work on other crops, already discussed, sometimes indicates a reduction of wilt with addition of potassium and with certain forms of nitrogen. Probably the balance of nutrients, as well as the form, is a factor here. Until more study is made on trees the only recourse is to maintain a good nutrient supply with the best balance known. Many affected trees probably will recover and make nearly normal growth under such conditions.

As already discussed, wilt is usually reported as less prevalent where the pH of the soil is lower, but there are certain conflicting reports. Furthermore, the change in pH required to achieve reduction in wilt is so great that pH adjustment does not seem feasible as a control measure.

Pruning and Wood Treatment. As noted earlier, there seems to be little danger of infection from inoculum carried on pruning tools. Much of the pruning is done when the temperature is too low for fungus growth, and the cuts are made smoothly which provides for rapid drying. Here again, in the absence of definite evidence, the practical operator cannot afford to spend a lot of time to prevent something that is unlikely to occur anyway.

Several authors suggest cutting out affected branches of trees. This seems to be usually a question of removing dead wood and branches weakened by the disease, but Gayford (43) suggests removing affected branches below the last sign of browning in the wood. He seems to imply that all of the infection may be removed in this manner. Wade (119) makes a similar suggestion, but states "... in many cases the disease enters through the roots, and the infection cannot be cut out." In this situation, probably more common, pruning accomplishes primarily the removal of weak branches that would be unlikely to recover.

Exclusion

This section refers primarily to planting only healthy trees in the orchard. Nursery trees should not be grown in fields where susceptible herbaceous crops have been grown. The possibility of the fungus being carried in the budwood should be examined, but until this is demonstrated to be a factor the practical grower cannot afford to take it into account. The propagator can avoid obviously affected trees in taking budwood, however.

Resistance

Resistance offers little help toward control of this disease on fruit trees. Most infections occur through the roots, and therefore the susceptibility of the rootstock largely determines severity of attack on the tree. As an extreme example, pear trees on quince rootstock may be killed, but it is doubtful that pear growing on a rootstock of a species of pear will be severely affected. The quince rootstock, however, is the only one available that is suitable for growing dwarf pear trees. For this reason it could not be given up as a rootstock for pear.

Plums growing on peach rootstock probably would be more severely affected than if they were on plum rootstock, but the peach is not a good rootstock for plum for other reasons also, and at least in the Northeast is not used extensively. On the other hand, peach on plum rootstock may be killed by Verticillium wilt, leaving the rootstock itself alive. Possibly, also, somewhat fewer infections of peach would occur on plum rootstock than on peach rootstock (30), but the peach is less expensive than plum rootstock to grow and generally provides a better root for the peach tree. Day (30) also reported Verticillium wilt as more severe on apricot on peach root than on Myrobalan. He reported it severe on apricot on apricot rootstock. He stated that apricot makes a better bud union on both peach and apricot rootstocks than on

Myrobalan. It seems, therefore, that the rootstock-scion combination is such a complex relationship that there is little chance to take advantage of resistance or tolerance to Verticillium in the selection of a rootstock. While control of this disease on stone fruits is far from satisfactory, measures such as sanitation, rotation, and cultural treatment seem to offer more immediate promise for study than does resistance.

On the other hand, in the case of avocado Zentmyer et al. (143) found the commonly used Mexican rootstock to be much less susceptible than the Guatemalan rootstock and suggested that the disease could become a serious problem on avocado if more use were made of the highly susceptible stocks. On a long term basis it might be worth while to examine the possibility of resistant rootstocks for the stone fruits.

DISCUSSION

There is ample evidence that Verticillium spp. may cause serious disease on many species of Prunus, but there is a great need for tests by direct inoculations to determine relative susceptibility. The symptoms of hadromycosis, however, are sufficiently diagnostic that most reports of disease occurrence can be accepted without reservation, particularly if the pathogen is isolated.

Verticillium hadromycosis, therefore, appears to be a disease that is potentially very serious on most or all species of stone fruits grown for commercial fruit production. It is endemic in most or all parts of the world where stone fruits are an important commerical crop and reaches epiphytotic proportions in some orchards. With such wide differences in incidence on neighboring farms (88) careful study of natural occurrence should yield valuable information on conditions that favor the disease and furnish suggestions for trial of measures to prevent severe outbreaks. Such a study could take advantage of the wealth of information in regard to Verticillium hadromycosis on other crops.

Among the pome fruits, the evidence is strong that quince (Cydonia oblonga), Photinia villosa, and the two species of Raphiolepis named are susceptible to hadromycosis caused by species of Verticillium, although experimental proof appears to be lacking. In these cases, however, the symptoms, both morphologic and anatomic, seem much like those described for certain of the stone fruits for which experimental evidence is ample. The fungus isolated from affected xylem tissue of these four pome fruit species appears identical with that isolated from proved hosts, although in no case were inoculations made to the same or to other species.

For pear the evidence is less convincing except that budlings on quince rootstock, of course, fail to survive or at least do not make satisfactory growth when the rootstock is affected. The report by Montemartini (89) is strongly suggestive but should be checked by inoculation experiments. The symptoms described do not resemble so closely those on stone fruits attacked by this fungus as do the symptoms on quince. On apple, the evidence is still less convincing. There is only one report of the isolation of any form of Verticillium from discolored wood in Malus pumila and inoculations failed to cause wilt.

It would be wise for practical purposes to consider the common quince, Raphiolepis spp., and Photinia villosa as susceptible. The chances of apple and pear being susceptible to this disease hardly appear to warrant consideration by the practical grower unless additional evidence is obtained.

Verticillium wilt is a disease of stone fruits that does not receive the attention it deserves. It is less common, of course, than such diseases as leaf-spot, brown rot, and some of the virus diseases and is frequently lost sight of. Unfortunately, sometimes individual orchards suffer very severe losses, particularly when the trees follow crops of tomato. Scattered occurrences in situations other than those associated with susceptible herbaceous crops may not be noticed at all or are diagnosed incorrectly. Often a grower could avoid losses by comparatively simple precautions, and the chief reason he does not follow a better practice is that he is not aware of the problem.

SUMMARY

All important commercial species of stone fruits are susceptible to Verticillium hadromycosis. No carefully controlled experiments have been made on differences in susceptibility but general experience gives us some rough comparisons. In the Northeast cherry and peach are damaged more than is plum. Elsewhere, almond and apricot also are highly susceptible. Among the pome fruits and related species, the common quince appears to be susceptible, as are two species of Raphiolepis and Photinia villosa. Possibly pear and apple are susceptible but only slightly so.

Apparently most severe outbreaks on stone fruits could be prevented if such trees were never planted following susceptible herbaceous crops, although there have been a few reports of severe incidence of the disease in the absence of such crops. Evidence indicates these outbreaks are most likely accounted for by susceptible weeds. A type of culture should be adopted that is capable of keeping such weeds under control because the fungus probably is carried into new fields in plant debris by winds and may build up there if susceptible herbaceous plants are present. Common weeds that have been named in this connection include Amaranthus spp., Chenopodium album, and Solanum spp.

If trees must be planted where susceptible crops have been grown in the immediate past presumably infection in the trees will be less if all possible plant debris is removed rather than plowed under.

Good cultural treatment should improve the ability of infected trees to recover. The possibility is discussed that antibiotic action in the soil as an aid in the reduction of amount of inoculum might be encouraged by growing suitable crops. Research is needed on this point.

Chemical fumigation of the soil has been disappointing and probably practical results depend as much on the influence of the fumigant on antagonistic fungi as on direct destruction of the wilt pathogen itself.

Resistance is not promising as a means of control of Verticillium wilt on fruit trees. Wide differences in susceptibility exist among species but closely related sorts do not appear to possess great differences. One species may be more severely affected when propagated on one rootstock than on another, but usually other considerations are sufficiently important that the grower could not afford to discontinue the use of the susceptible rootstock for this reason alone.

Literature Cited:

1. ADAMS, R. E., and S. E. TAMBURO. 1957. The West Virginia spot-rot complex of apple in 1956. Plant Disease Reptr. 41: 760-765.
2. ANONYMOUS. 1931. Maladies des arbres et arbustes fruitiers. In Rapport sur le fonctionnement de l'Inst. des Recherches Agron. pendant l'année 1930, vol. 9: 430-434.
3. ANONYMOUS. 1932. Dépérissement de l'abricotier. In Rapports sommaires sur les travaux accomplis dans les laboratories en 1931. Ann. Épiphyt. 18: 54-96. [Pertinent part on pp. 85-86].
4. ANONYMOUS. 1943. Plant diseases and insect pests. Notes by the Biological Branch. Jour. Dep. Agr., Victoria 41: 365-370.
5. ANONYMOUS. 1956. Verticillium-wilt of apricot. Ann. Rep. Dept. Sci. and Ind. Research, New Zealand 20: 23.
6. ANONYMOUS. 1950. Plant disease and pest investigations. Ann. Rep. Dept. Sci. and Ind. Research, New Zealand 24: 63-70.
7. ANONYMOUS. 1951. Enige ziekte en plagen in cultuurgewassen in 1950 en hun bestrijding. Verslag. en Meded. van de Plantenziek. Dienst te Wageningen, no. 118, pp. 1-120. [Pertinent parts on pages 18, 38, and 56.]
8. ARK, P. A., and MARJORIE L. HUNT. 1941. Saprophytes antagonistic to phytopathogenic and other microorganisms. Science 93: 354-355.
9. ARNSTEIN, H. R. V., A. H. COOK, and MARGARET S. LACEY. 1948. The inhibition of Fusarium oxysporum var. cubense by musarin, an antibiotic produced by Meredith's actinomycete. Jour. Gen. Bact. 2: 111-122.
10. ATANASOFF, D., D. N. DODOFF, IV. CHR. KOVACHEVSKY, ST. IV. MARTINOFF, V. TRIFONOVA, and AL. CHRISTOFF. 1932. [Parasitic fungi new for Bulgaria.] Annuaire de l'Université de Sofia V. Faculté D'Agronomie et de Sylviculture 10: 341-366. (English summary.) [Part of original translated for the writer by Robert Herr.]
11. BEREND, ISTVÁN. 1955. Újabb adatok a kajszibarackfák verticilliózisos pusztulásához. Növénytermelés 4: 285-288. [Recent data about the Verticillium-wilt of apricot trees. Abstract in Hungarian Agric. Review 5 (1): 12. 1956.]

12. BERKELEY, G. H., G. O. MADDEN, and R. S. WILLISON. 1931. Verticillium wilts in Ontario. Sci. Agr. 11: 739-759.
13. BLANK, LESTER M., and PHILIP J. LEYENDECKER, Jr. 1951. Verticillium wilt spread to disease-free soil by infected cotton stalks. Plant Disease Reptr. 35: 10-11.
14. BLODGETT, EARLE C., and JAMES A. TWOMEY. 1955. Verticillium wilt of orchard trees. Wash. State Hort. Assoc. Proc. 51: 146-148.
15. BONGINI, VIRGINIA. 1953. Cuor nero del legno di albicocco (Prunus armeniaca.) [Black heart of the wood of apricot.] In Segnalazioni fitopatologiche. Suppl. Annali della sper. Agraria, n. s. 7 (3): XXVII-XXVIII.
16. BRIEN, R. M. 1946. Second supplement to "A list of plant diseases recorded in New Zealand." New Zealand Jour. Sci. and Technol., Sect. A, 28: 221-224.
17. BRIEN, R. M., and JOAN M. DINGLEY. 1951. A revised list of plant diseases recorded in New Zealand. New Zealand Dept. Sci. and Ind. Research Bull. 101: 1-62.
18. BRIEN, R. M., and JOAN M. DINGLEY. 1952-1953. First supplement to "A revised list of plant diseases recorded in New Zealand" 1949-51. New Zealand Jour. Sci. and Technol., Sect. A, 34: 556-562.
19. BRIEN, R. M., and JOAN M. DINGLEY. 1955. Second supplement to "A revised list of plant diseases recorded in New Zealand," 1952-1955. New Zealand Jour. Sci. and Technol., Sect. A, 37: 27-35.
20. BRODSKY, A. L. 1941. Antagonistische Beziehungen zwischen den Bodeninfusorien und dem pathogenen Bodenpilz. Compt. Rend. (Doklady) Acad. Sci. U.R.S.S. 33: 81-83. [Published in German in the original, from translation by A. Gurewitsch.]
21. CAROSELLI, NESTOR E. 1957. Verticillium wilt of maples. Rhode Island Univ., Agr. Exp. Sta. Bull. 335: 1-84.
22. CARRERA, CÉSAR. 1939. Un caso de "verticilliosis" aparacido y comprobado sobre ciruelo en la provincia de Buenos Aires. Congreso Fruitcola de San Juan 4 (1936): 334-341.
23. CARTER, J. C. 1938. Verticillium wilt of woody plants in Illinois. Plant Disease Reptr. 22: 253-254.
24. CHABROLIN, CH. 1928. Notes et observations relatives aux dépérissements de l'abricotier. Ann. Épiphyt. 14: 355-376.
25. CHABROLIN, CH. 1929. Les dépérissements de l'abricotier. Compt. Rend. Acad. Agr. France 15: 583-588.
26. CHENEY, GWENDOLYN M. 1930. "Black-heart" of apricots in Victoria. Australian Jour. Exp. Biol. and Med. Sci. 7: 91-100.
27. CONNERS, I. L., and D. B. O. SAVILE. 1945. Twenty-fourth Annual Report of the Canadian Plant Disease Survey, 1944: i-xviii; 1-122.
28. CONNERS, I. L., and D. B. O. SAVILE. 1953. Thirty-second Annual Report of the Canadian Plant Disease Survey, 1952: i-xviii; 1-123.
29. CURZI, M. 1930. Intornó alle tracheomicosi e a nuovi gravi casi di verticilliosi. Boll. Regia Staz. Patol. Vegetale, N. S., 10: 44-62.
30. DAY, LEONARD H. 1953. Rootstocks for stone fruits. Observations and experiments with plum, peach, apricot, and almond roots for stone fruits. Calif. Univ. Agr. Exp. Sta. Ext. Serv. Bull. 736: 1-76.
31. DELMAS, H. G. 1952. Quelques aspects de la culture de l'abricotier en France. Fruits (Paris) 7: 311-323.
32. De SEGURA, C. BAZÁN, and PEDRO AGUILAR F. 1955. Nematodes and root rot diseases of Peruvian cotton. Plant Disease Reptr. 39: 12.
33. DIMOCK, A. W. 1951. Bud transmission of Verticillium in roses. Phytopathology 41: 781-784.
34. DOCHINGER, L. S. 1956. New concepts of the Verticillium wilt disease of maple. (Abstr.) Phytopathology 46: 467.
35. DOCHINGER, L. S. 1956. A study of the Verticillium wilt disease of maple trees. Dissertation Abstr. 16: 2262.

36. DONANDT, SIEGFRIED. 1931-1932. Untersuchungen über die Pathogenität des Wirtelpilzes Verticillium alboatrum R. U. B. Zeit. Parasitenk. 4: 653-711.

37. DUFRENOY, J. 1927. Dépérissement des arbres fruitiers dans le Massif Central. Bull. l'Office Agric. Régional du Massif Central 8 (1926): 103-113.

38. DUFRENOY, J., and M. L. DUFRENOY. 1927. Hadromycoses. Ann. Épiphyt. 13: 195-212.

39. DUFRENOY, M. 1927. Recherches relatives au dépérissement des arbres fruitiers. Bull. Trim. Office Régional Agricole du Midi 23: 176-178.

40. EDGINGTON, LLOYD V. 1957. Temperature and nutritional studies on Verticillium and Fusarium wilts of tomato. Dissertation Abstr. 17: 22.

41. ENGLEHARD, ARTHUR W. 1957. Host index of Verticillium albo-atrum Reinke & Berth. (including Verticillium dahliae Kleb.). Plant Disease Reptr. Suppl No. 244: 23-49.

42. GAUDINEAU, MARGUERITE. 1949. Sur quelques maladies parasitaires (pourridiés - plombs - flétrissements) et leur incidence dans la "mortalité des pruniers." II^e Congrès National de la Prune et du Pruneau, Agen 1948, pp. 99-103.

43. GAYFORD, G. W. 1950. Orchard notes. Jour. Dept. Agr., Victoria 48: 169-170.

44. GHILLINI, C. A. 1937. Infezioni vasali nelle piante coltivate: la trombosi da "verticillium" nella varieta "Prunus Davidiana." Italia Agricola 74: 208-210.

45. GODFREY, G. H. 1936. Control of soil fungi by soil fumigation with chlorpicrin. Phytopathology 26: 246-256.

46. GOHEEN, AUSTIN C. 1949. Verticillium wilt on apricots in Washington State. Plant Disease Reptr. 33: 99.

47. GOIDÁNICH, GABRIELE. 1932. La verticilliosi dell' "Acer campestre" L. e alcuni altri casi di tracheomicosi in Italia. Boll. Regia Staz. Patol. Vegetale, N.S. 12: 285-287. [The verticilliosis of Acer campestre L. and some other cases of tracheomycoses in Italy. Translation, B. P. I. no. 254, in U. S. Dept. of Agr. Library, translated by G. Manganaro.]

48. GOIDÁNICH, GABRIELE. 1935. Nuovi casi di trachemicosi da "Verticillium" in Italia. Osservazioni su una specie nuova di "Verticillium" tracheicolo. Boll. Regia Staz. Patol. Vegetale, N. S. 15: 548-554. [New cases of tracheomycosis caused by Verticillium in Italy. Observations on a new species of tracheid-inhabiting Verticillium. Translation, B. P. I. No. 258, in U. S. Dept. of Agr. Library, translated by G. Manganaro. The translation is limited to parts of pp. 549-550.]

49. GREEN, RALPH J., Jr., and JOHN V. LUCK. 1954. Effect of soil fumigation and planting stock on Verticillium wilt of peppermint. (Abstr.) Phytopathology 44: 490.

50. HAENSELER, C. M. 1928. Effect of soil reaction on Verticillium wilt of eggplant. Forty-ninth Ann. Rept. New Jersey State Agr. Exp. Sta. for the year ending June 30, 1928: 267-273.

51. HESSE, CLARON O. 1952. Apricot culture in California. Section V -- Diseases and pests. Calif. Univ., Agr. Exp. Sta. Ext. Serv. Circ. 412: 1-12.

52. HOCHAPFEL, H. 1954. Verticilliose an Steinobst. Jahresbericht. der Biol. Bundesanstalt für Land- und Forstwirtschaft in Braunschweig, 1952: 77.

53. HOLMES, F. W. 1955. Field and culture tests of antibiotics against Graphium ulmi. (Abstr.) Phytopathology 45: 185.

54. HORNBOSTEL, W. 1939. Versuche über Wurzelkropfbekämpfung. Zeit. Pflanzenkr. 49: 1-11.

55. HUBER, GLENN A. 1932. The fungi present on the surfaces of normal apples and their relation to decay. (Abstr.) Phytopathology 22: 13.
56. HUSZ, BÉLA. 1947. Mikólogiai vizsgálatok pusztuló kajszifákon. Acta Mycol. Hung. 4 (1-2): 6-12. [Mycological investigations on apoplectic apricot trees. English summary.]
57. HUTTON, K. E., and J. R. MORSCHEL. 1954. Black heart of apricots in N. S. W. Agr. Gaz., N. S. Wales 65: 364-367.
58. ISAAC, IVOR. 1946. Verticillium wilt of sainfoin. Ann. Appl. Biol. 33: 28-34.
59. ISAAC, IVOR. 1949. A comparative study of pathogenic isolates of Verticillium. Brit. Mycol. Soc. Trans. 32: 137-157.
60. ISAAC, IVOR. 1953. Studies in the interactions between species of Verticillium. Ann. Appl. Biol. 40: 623-629.
61. ISAAC, IVOR. 1954. Studies in the antagonism between Blastomyces luteus and species of Verticillium. Ann. Appl. Biol. 41: 305-310.
62. ISAAC, IVOR. 1956. Some soil factors affecting Verticillium wilt of Antirrhinum. Ann. Appl. Biol. 44: 105-112.
63. ISAAC, IVOR. 1957. The effects of nitrogen supply upon the Verticillium wilt of Antirrhinum. Ann. Appl. Biol. 45: 512-515.
64. ISAAC, IVOR. 1957. Wilt of lucerne caused by species of Verticillium. Ann. Appl. Biol. 45: 550-558.
65. JOESSEL, P. H. 1928. Quelques maladies du pêcher et de l'abricotier dans la region rhodanienne (1). Progr. Agr. et Vit. 90: 370-374.
66. JOESSEL, P. H., and J. BORDAS. 1931. Recherches sur les dépérissements de l'abricotier dans la valée du Rhone (1) (1927 à 1930). Ann. Épiphyt. 17: 325-361.
67. JUNE, R. I. 1950. Verticillium wilt of stone fruit. New Zealand Jour. Agr. 81: 307-308.
68. KEYWORTH, W. G. 1942. Verticillium wilt and virus diseases of the hop. Ann. Appl. Biol. 29: 323-324.
69. KEYWORTH, W. G. 1942. Verticillium wilt of the hop (Humulus lupulus). Ann. Appl. Biol. 29: 346-357.
70. KEYWORTH, W. G. 1944. Verticillium wilt of plum. Ann. Rep. East Malling Research Sta., Kent 31 (1943): 52-54.
71. KLEBAHN, H. 1913. Beiträge zur Kenntnis der Fungi Imperfecti. I. Eine Verticillium-Krankheit auf Dahlien. Mycol. Centralbl. 3 (2): 49-66.
72. KONONENKO, E. V. 1937. [Lysis of the causal organism of cotton wilt, Verticillium dahliae, induced by certain myxobacteria.] Mikrobiologiia 6: 699-716. [English summary, and table listing soils and figure legends are translated into English. Title and main text of paper in Russian.]
73. KREUTZER, W. A., and J. Th. W. MONTAGNE. 1950. Chlorobromopropene, a potential fungicidal soil fumigant. (Abstr.) Phytopathology 40: 16.
74. KUBLANOVSKAIA, Mme G. M. 1952. Ob ispol'zovanii Aktinomitsetov-antagonistov protiv fuzarioznogo uviadaniia khlopchatnika. Mikrobiologiia 21: 340-347. (On use of Actinomycetes-antagonists against Fusarium wilt of cotton. U. S. Dept. of Agr. Library translation No. 7880, translated by A. Antik).
75. LEBEN, CURT, G. J. STESSEL, and G. W. KEITT. 1952. Helixin, an antibiotic active against certain fungi and bacteria. Mycologia 44: 159-169.
76. LEONT'EV, I. F. 1948. Fungit͡sidnye svoĭstva infuzoriĭ. Priroda [Nature] 6: 58-59. [Fungicidal properties of infusoria. U. S. Dept. of Agr. translation no. 7747, translated by A. Antik.]
77. LONA, FAUSTO. 1939. Nuovi casi di tracheoverticilliosi su Digitalis lanata e Santolina chamaecyparissus. Atti Ist. Botanico "Giovanni Briosi" Lab. Crittogam., Univ. Pavia, Ser. IV, 11: 273-288. (Latin and English summaries.)

78. LUCK, JOHN V. 1954. Studies on the Verticillium wilt of Mentha piperita L., with special emphasis on the causal organism, Verticillium albo-atrum R. & B. Dissertation Abstr. 14: 916-917.
79. LUDBROOK, W. V. 1933. Pathogenicity and environal studies on Verticillium hadromycosis. Phytopathology 23: 117-154.
80. McCLELLAN, W. D., STEPHEN WILHELM, and ALAN GEORGE. 1955. Incidence of Verticillium wilt in cotton not affected by root-knot nematodes. Plant Disease Reptr. 39: 226-227.
81. McINTOSH, D. L. 1954. Verticillium wilt of sweet cherry in British Columbia. Plant Disease Reptr. 38: 74-75.
82. McKAY, M. B. 1926. Further studies of potato wilt by Verticillium albo-atrum. Jour. Agr. Res. 32: 437-470.
83. McKEEN, COLIN D. 1943. A study of some factors affecting the pathogenicity of Verticillium albo-atrum R. & B. Canad. Jour. Research, Sect. C, 21: 95-117.
84. McKEEN, W. E., and J. E. BOSHER. 1955. Verticillium wilt of strawberries in British Columbia. Plant Disease Reptr. 39: 371-372.
85. MARCHAL, É. 1932. Recherches et observations effectuées à la Station de Phytopathologie de l'État pendant la période 1927-1931. Bull. Inst. Agron. et Sta. Recherches Gembloux 1: 164-174. [See p. 170 only.]
86. MARCHAL, É. 1933. Observations et recherches effectuées à la Station de Phytopathologie de l'État pendant l'année 1932. Bull. Inst. Agron et Sta. Recherches Gemblous 2: 147-159. [See pp. 155 only.]
87. MILLER, PAUL R., and NELLIE W. NANCE. 1949. Preliminary estimates of acreages of crop lands in the United States infested with some organisms causing plant diseases. Plant Disease Reptr. Suppl. no. 185: 207-252.
88. MILLS, W. D. 1932. Occurrence of Verticillium wilt of peach in New York. Plant Disease Reptr. 16: 132-133.
89. MONTEMARTINI, LUIGI. 1935. Note di fitopatologia. Riv. Patol. Vegetale 25: 25-31.
90. MORVAN, G. 1956. Le dépérissement de l'abricotier. I. Les différentes formes de dépérissement. Ann. Épiphyt., Ser. C, 7: 211-227.
91. NELSON, RAY. 1950. Verticillium wilt of peppermint. Mich. State Univ., Agr. Exp. Sta. Tech. Bull. 221: 1-259.
92. NOBLE, MARY, N. F. ROBERTSON, and W. J. DOWSON. 1953. Verticillium wilt of lucerne in Britain. Plant Pathol. 2: 31-33.
93. POLLACCI, GINO. 1933. Rassegna sull' attività del R. Laboratorio Crittogamico di Pavia (Osservatorio fitopatologico per le provincie di Cremona, Parma, Pavia e Piacenza) durante l'anno 1932. Atti Ist. Bot. "Giovanni Briosi" e Lab. Crittogam., Univ. Pavia, Ser. IV, 4: 283-287.
94. PRESLEY, JOHN T. 1950. Verticillium wilt of cotton with particular emphasis on variation of the causal organism. Phytopathology 40: 497-511.
95. RAABE, ROBERT D., and STEPHEN WILHELM. 1955. Field studies of rose rootstock infections by the Verticillium wilt fungus. (Abstr.) Phytopathology 45: 695.
96. REHDER, ALFRED. 1940. Manual of cultivated trees and shrubs hardy in North America. Second edition. 996 pp. MacMillan, New York.
97. REHDER, ALFRED. 1949. Bibliography of cultivated trees and shrubs hardy in the cooler temperate regions of the Northern Hemisphere. 825 pp. Arnold Arboretum, Jamaica Plain, Mass.
98. RENOUF, L. R. 1948. Verticillium wilt of apricots. New Zealand Jour. Agr. 77: 284.
99. RICHTER, H., and M. KLINKOWSKI. 1938. Wirtelpilz-Welkekrankeit an Luzerne und Esparsette. NachrBl. deut. Pflanzenschutzdienst (Berlin) 18: 57-58.

100. RIEUF, P. 1950. Le dépérissement des abricotiers. I. État des recherches en France et à l'etranger. II. Situation et recherches au Maroc. Fruits et Primeurs 20: 354-357; 393-395.

101. ROBERTS, F. M. 1943. Factors influencing infection of the tomato by Verticillium albo-atrum. Ann. Appl. Biol. 30: 327-331.

102. ROBINSON, D. B., R. H. LARSON, and J. C. WALKER. 1947. Verticillium wilt of potato in relation to symptoms, epidemiology and variability of the pathogen. Wisconsin Univ., Agr. Exp. Sta. Research Bull. 202: 1-49.

103. RUDOLPH, B. A. 1926. Verticillium wilt of tomatoes in California. Phytopathology 16: 234.

104. RUDOLPH, B. A. 1931. Verticillium hadromycosis. Hilgardia 5: 197-353.

105. SAREJANNI, J. A. 1935. L'apoplexie des arbres fruitiers des environs d'Athènes. Ann. Inst. Phytopath., Benaki, [Greece] 1 (3): 45-50.

106. SCHNEIDER, HENRY. 1048. Susceptibility of guayule to Verticillium wilt and influence of soil temperature and moisture on development of infection. Jour. Agr. Res. 76: 129-143.

107. SMITH, H. C. 1951. Verticillium wilt of apricot, gooseberry, strawberry, and tomato. New Zealand Jour. Agr. 83: 129-130.

108. SOLOVEVA, Mme A. I., and Mme L. V. POLYARKOVA. 1940. [Wilt of cotton.] Tashkent Agr. Publ. Dept., Uzbekistan Soviet Republic. 63 pp. [Title and article in Russian. Pertinent parts translated for the writer by Robert Herr.]

109. SOMMER, H. 1936. Nochmals: Ahornsterben in der Baumschule. Der Blumen-und Pflanzenbau vereinigt mit der Gartenwelt 40: 566-567.

110. SPRAGUE, RODERICK. 1957. Fungi isolated from roots and crowns of pear trees. Plant Disease Reptr. 41: 74-76.

111. STRONG, FORREST C. 1938. Prevalence of wilt diseases in maple and elm. Mich. State Coll., Agr. Exp. Sta. Quart. Bull. 21: 96-99.

112. VAN DEN ENDE, G. 1956. De reacties van verschillende waardplanten bij aantasting door Verticillium sp. (Abstr.) Tijdschr. Plantenziekten 62: 21.

113. VAN DER LEK, H. A. A. 1918. Over de z.g. "Verwelkingsziekten in het bijonder die, welke door Verticillium alboatrum veroorzaakt worden. Tijdschr. Plantenziekten 24: 205-219.

114. VAN DER MEER, J. H. H. 1925. Verticillium-wilt of herbaceous and woody plants. Mededeel. Landbouwhoogeschool Wageningen 28 (2): 1-82.

115. VAN DER MEER, J. H. H. 1926. Verticillium-wilt of maple and elm-seedlings in Holland. Phytopathology 16: 611-614.

116. VANDERWALLE, R. 1939. Un cas de verticilliose sur cognassier. Bull. Inst. Agron. et Sta. Recherches Gembloux 8: 106-110.

117. VAN KOOT, Y. 1947. Verschillende oorzaken van afsterving van perziken en pruimen onder glas. Meded. Direct. Tuinb. 10: 618-634.

118. VERNER, A., P. MALYSHKIN, and N. KVINT. 1941. Development of fungi in the soil. Compt. Rend. (Doklady) Acad. Sci. U. R. S. S., New Series, 31: 812-814. [Published in English in the original, from translation by D. Rakhmanov.]

119. WADE, G. C. 1949. Apricot diseases. Tasmanian Jour. Agr. 20: 22-29.

120. WEISS, FREEMAN, and MURIEL J. O'BRIEN. 1953. Index of plant diseases in the United States. Part V. Pinaceae-Zygophyllaceae. U. S. Dept. Agr., Plant Disease Survey Special Publ., Number 1, pp. 807-1192.

121. WELTZIEN, HEINRICH C. 1957. Untersuchungen über das Vorkommen der Luzernevertizilliose und weiter Luzerneerkrankungen in Südwestdeutschland. NachrBl. deut. Pflanzenschutzdienstes (Stuttgart) 9: 42-45.

122. WILHELM, STEPHEN. 1948. The effect of temperature on the taxonomic characters of Verticillium albo-atrum Rke. et Bert. (Abstr.) Phytopathology 38: 919.

123. WILHELM, STEPHEN. 1950. Vertical distribution of Verticillium albo-atrum in soils. Phytopathology 40: 368-376.

124. WILHELM, STEPHEN. 1950. Verticillium wilt in acid soils. Phytopathology 40: 776-777.

125. WILHELM, STEPHEN. 1951. Effect of various soil amendments on the inoculum potential of the Verticillium wilt fungus. Phytopathology 41: 684-690.

126. WILHELM, STEPHEN. 1951. Is Verticillium albo-atrum a soil invader or a soil inhabitant? (Abstr.) Phytopathology 41: 944-945.

127. WILHELM, STEPHEN. 1955. Some factors affecting substrate colonization and growth of the Verticillium wilt fungus in soil. (Abstr.) Phytopathology 45: 696.

128. WILHELM, STEPHEN. 1955. Longevity of the Verticillium wilt fungus in the laboratory and field. Phytopathology 45: 180-181.

129. WILHELM, STEPHEN. 1957. Determining the inoculum potential of Verticillium in soil and predicting subsequent wilt losses in strawberry. (Abstr.) Phytopathology 47: 37.

130. WILHELM, STEPHEN. 1957. Chloropicrin gives promising control of Verticillium wilt in strawberry. (Abstr.) Phytopathology 47: 37.

131. WILHELM, STEPHEN, and JOHN FERGUSON. 1953. Soil fumigation against Verticillium albo-atrum. Phytopathology 43: 593-596.

132. WILHELM, STEPHEN, GEORGE NYLAND, and FRED CHARLES. 1954. Verticillium wilt of sweet cherry in California. Plant Disease Reptr. 38: 438.

133. WILHELM, STEPHEN, ROBERT D. RAABE, and EUGENE B. SMALLEY. 1955. Some previously unrecorded hosts of Verticillium albo-atrum in California. Plant Disease Reptr. 39: 693-694.

134. WILLISON, R. S. 1933-1934. Peach canker investigations. I. Some notes on incidence, contributing factors and control measures. Sci. Agr. 14: 32-47.

135. WILLISON, R. S. 1937. Peach canker investigations. III. Further notes on incidence, contributing factors, and related phenomena. Can. Jour. Research, Sect. C, 15: 324-339.

136. WILSON, KENNETH S. 1954. The fate of Verticillium albo-atrum R. & B. in muck soil as affected by various species of fungi. Dissertation Abstr. 14: 1516.

137. WOLLENWEBER, H. W. 1929. Die Wirtelpilz-Welkenkrankheit (Verticilliose) von Ulme, Ahorn und Linde usw. Arb. Biol. Reichsanstalt Land- u. Forstwirtsch. 17: 273-299. [On the verticilliosis of elm, maple, linden, etc. Translation B. P. I. no. 796 in U. S. Dept. of Agr. Library, translated by A. H. Krappe.]

138. WORMALD, H., and R. V. HARRIS. 1932. Notes on plant diseases in 1931. Cherry. Gardneners' Chronical, Third Series, 91: 207-208.

139. WORMALD, H., and R. V. HARRIS. 1933. Notes on plant diseases in 1932. Gardeners' Chronical, Third Series, 93: 192-193.

140. WORMALD, H., and R. V. HARRIS. 1937. Notes on plant diseases in 1936. Ann. Rep. East Malling Research Sta., Kent 24 (1936): 187-193.

141. WORMALD, H., and R. V. HARRIS. 1938. Notes on plant diseases in 1937. Ann. Rep. East Malling Research Sta., Kent 25 (1937): 181-186.

142. ZELLER, S. M. 1936. Verticillium wilt of cane fruits. Oregon State Coll., Agr. Exp. Sta. Bull. 344: 1-25.

143. ZENTMYER, G. A., F. F. HALMA, and STEPHEN WILHELM. Relative susceptibility of Guatemalan and Mexican avocado rootstocks to Verticillium wilt. Phytopathology 45: 635-636.

CORNELL UNIVERSITY, ITHACA, NEW YORK